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Neuronal plasticity in the development of birds

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Many studies have demonstrated that both the physiological properties and the morphological features of neurons of the mammalian visual cortex are influenced by sensory input during early development. The classical example is provided by the studies of Hubel and Wiesel (1970) who showed that monocular deprivation of young cats alters the balance of inputs to cortical neurons. In normally raised adult cats most neurons of area 17 are driven by both eyes, whereas monocular deprivation leads to a substantial loss of input from the deprived eye so that most cortical neurons of deprived animals are almost exclusively driven by the intact eye.

Other experiments have demonstrated that the physiological changes which are induced by monocular deprivation are accompanied by morphological alterations, for example by changes in number and size of cortical synapses (Winfield, 1983, Cragg, 1975) or LGN cell size (Wiesel and Hubel, 1963). These effects can only be observed if the change in sensory input occurs during a limited period, early in the animals development. After this time, alteration of physiological or morphological features of visual cortex neurons is much more difficult (Blakemore and Van Sluyters, 1974). Consequently, the changes induced during the sensitive period are remarkably stable.

In contrast to mammals, it is only recently that the developmental plasticity of avian neurons has received attention. Pettigrew and Konishi (1976) demonstrated that neurons in the visual wulst, the end station of the thalamofugal pathway of owls, have the same physiological characteristics as the visual cortex of mammals with respect to binocularity and receptive field properties. Pettigrew and Konishi also demonstrated that monocular deprivation in owls induces the same shift in ocular dominance in the visual wulst as it was demonstrated for the visual cortex in cats and monkeys.

However, owls are very untypical representatives of the avian phylum. Unlike the majority of birds they have frontally instead of laterally placed eyes. In birds with laterally placed eyes, the thalamofugal pathway is not well developed, and the tectofugal pathway seems to adopt many tasks of visual processing which are performed by the geniculocortical pathway in mammals, although these two pathways in birds and mammals are not homologous (Karten, 1969).

We examined the effects of monocular deprivation on the tectofugal pathway of the zebra finch, a small bird with laterally placed eyes. This bird was chosen, because it has been the subject of very detailed studies of sexual imprinting which has, at least at the descriptive level, many similarities whith cortical plasticity (Bischof 1983, 1985 a,b). Sexual imprinting is a learning process by which young birds learn the image of the species which they will court as adults. Like the developmental plasticity of cortical neurons,

learning occurs during a sensitive period in early development and the information which is stored during this sensitive period is remarkably resistant to forgetting. Moreover, other similarities as e.g. dependency of storage on motivational factors can be demonstrated in both paradigms.

On the basis of these similarities, I speculated that both, cortical plasticity and sexual imprinting, are an expression of a common developmental process by which neuronal networks are exactly adapted to the processing of environmental features (Bischof, 1983, 1985a,b). If this hypothesis is true, effects of monocular deprivation in zebra finches, which as like as in mammals should affect directly the wiring of sensory areas, should be at least roughly restricted to the time of development where imprinting occurs, i.e. the sensitive periods of both paradigms should be similar.

In this paper, I shall summarize the results which my research group collected on the development of the tectofugal system and the effects of monocular deprivation in zebra finches. These results will be discussed in the context of sexual imprinting and compared with the findings of other research groups investigating the physiological basis of imprinting and its anatomical location within the brain of birds. As I will demonstrate in the discussion, at least some of the results are compatible, although the rationale of the different research groups is rather different.

Material and methods

All experiments described here were performed with zebra finches obtained from the institute's stock. The methods used in the experiments are fully described elsewhere (Herrmann and Bischof, 1988a,b,c, 1988a,b, Nixdorf and Bischof, 1986, 1987). We examined the development and developmental plasticity of morphological features of neurons and synapses in n. rotundus and ectostriatum of normal birds as well as monocularly deprived animals. Deprivation was performed by either closing the eyelids with medical adhesive or, in most cases, by application of a light tight plastic cap over one eye. Light microscopic methods included measurements of neuronal size in Nissl stained sections, as well as estimations of dendrite ramification, radius of the dendritic field, and density of spines in Golgi preparations. In electron microscopic preparations, the density of synapses, the length of the postsynaptic thickening, and the size of the presynaptic terminal was calculated. In addition, we used several track-tracing methods and electrophysiological experiments to examine in more detail the influence of connections of the ipsilateral eye on the development and function of the tectofugal pathway, since the deprivation experiments implied that in contrast to earlier statements projections from the ipsilateral eye are important for visual processing within the tectofugal pathway.

Results

1. Behavioral development

Zebra Finches are altricial birds and their eyes open 5 or 6 days after hatching. By ten days of age the young can react to visual stimuli and by 15 days of age they are able to discriminate between different stimuli (Bischof and Lassek 1985). Fledging occurs between 18 and 20 days, the birds become independent from their parents at 35 days and reach sexual maturity by the 100th day. The sensitive period for sexual imprinting starts at about 10 days, reaches a peak at day 15 and slopes down until day 25 (Fig. 1, Immelmann, 1972).

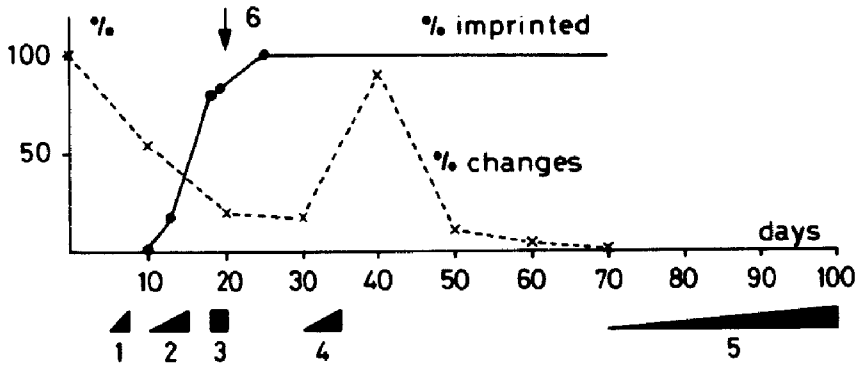

Fig. 1: Features of Zebra Finch development. Solid line: Sensitive period for imprinting – percentage of birds which revealed to be imprinted at a given time. Stippled line: Sensitive period for monocular deprivation – further explanations see fig. 8. 1: time of eye opening, 2: increase of visual performance, 3: fledging, 4: independence from parents, 5: sexual maturity, 6: peak in development of neuronal elements.

2. The tectofugal pathway

The first station of the tectofugal pathway, the optic tectum, receives input from the contralateral eye via the optic nerve. Ipsilateral retinotectal projections have been described only for very young birds, e. g. in pigeons. In adult birds no such projection can be observed (Bagnoli et al, 1987). On the basis of these findings it has been thought that the tectofugal pathway only processes contralateral information.

Visual information from the tectum is processed further by the n. rotundus of the thalamus and then by the telencephalic target area of the pathway, the ectostriatum. From this area, information is most probably processed further by other telencephalic areas. However, no details are known about these projections. Fig. 2 depicts the main stations of the tectofugal pathway and shows some interhemispheric connections, which in the past have been considered to be minor, but have become important in the course of our experiments.

3. Normal development

Althouth our results concerning the development of the tectofugal pathway are far from complete, they give some hints about the general development of two of the nuclei of the pathway, the n. rotundus and the ectostriatum. As far as data are available, the two nuclei seem to develop almost in parallel. However, there are some exceptions. Fig. 3 summarizes the data we obtained from light microscopic investigations. Fig. 3a (Herrmann and Bischof, 1986a) shows the development of neuron size in the n. rotundus (solid line) and the ectostriatum (stippled line). The next figures (Herrmann and Bischof, 1988b) depict the development of the main type of ectostriatal neurons (Fig. 3b) as revealed by the Golgi method: the radius of the dendritic field, the number of terminals per primary dendrite (Fig. 3c), and the number of spines/10μ of dendritic length (Fig. 3d) for different segments of the dendrites.

It is obvious that all light microscopically investigated parameters we have measured increase very rapidly from day 5 to day 20. All neuronal elements show a peak at day 20 and a subsequent significant decrease between day 20 and 40. Overshoot and subsequent reduction can also be observed in some ultrastructural parameters, (Fig. 4). Fig. 4a shows

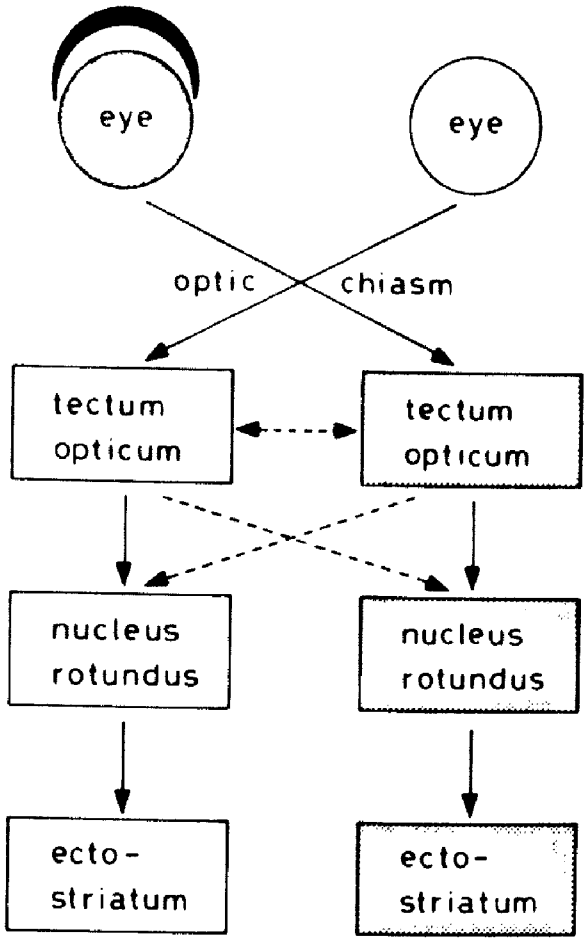

Fig. 2: Tectofugal pathway of birds. The cap over one eye symbolizes deprivation. Stippled areas: deprived eye and brain areas. Due to the complete crossing of the optic nerve in the chiasm, monocular deprivation creates a deprived hemisphere contralateral to the deprived eye.

the development of the number of synapses per 1000 μm^2 for the n. rotundus (solid line) and ectostriatum (stippled line), Fig. 4b the development of the length of the postsynaptic thickenings for n. rotundus and ectostriatum. The development of the density of synapses parallel those parameters detected under the light microscope as does the development of the length of postsynaptic thickenings of the ectostriatum. In contrast, the length of the postsynaptic thickenings in n. rotundus decreases from day 5 until adulthood. A third ultrastructural parameter, the size of the presynaptic area, increases for n. rotundus until day 20 and thereafter remains constant, whereas it increases until day 100 in the ectostriatum (Fig. 4c).

The decrease of the length of the postsynaptic thickening from day 1, which is observed in the n. rotundus, may indicate that the peak value of development could be observed before hatching, and the plateau in the development of presynaptic terminal size is obviously reached earlier in n. rotundus. Thus, these differences might suggest that the n. rotundus develops earlier than the ectostriatum.

4. Monocular deprivation

For these studies the birds were deprived monocularly shortly after birth (before natural eye opening) for 20, 40, or 100 days and were sacrificed immediately after the deprivation

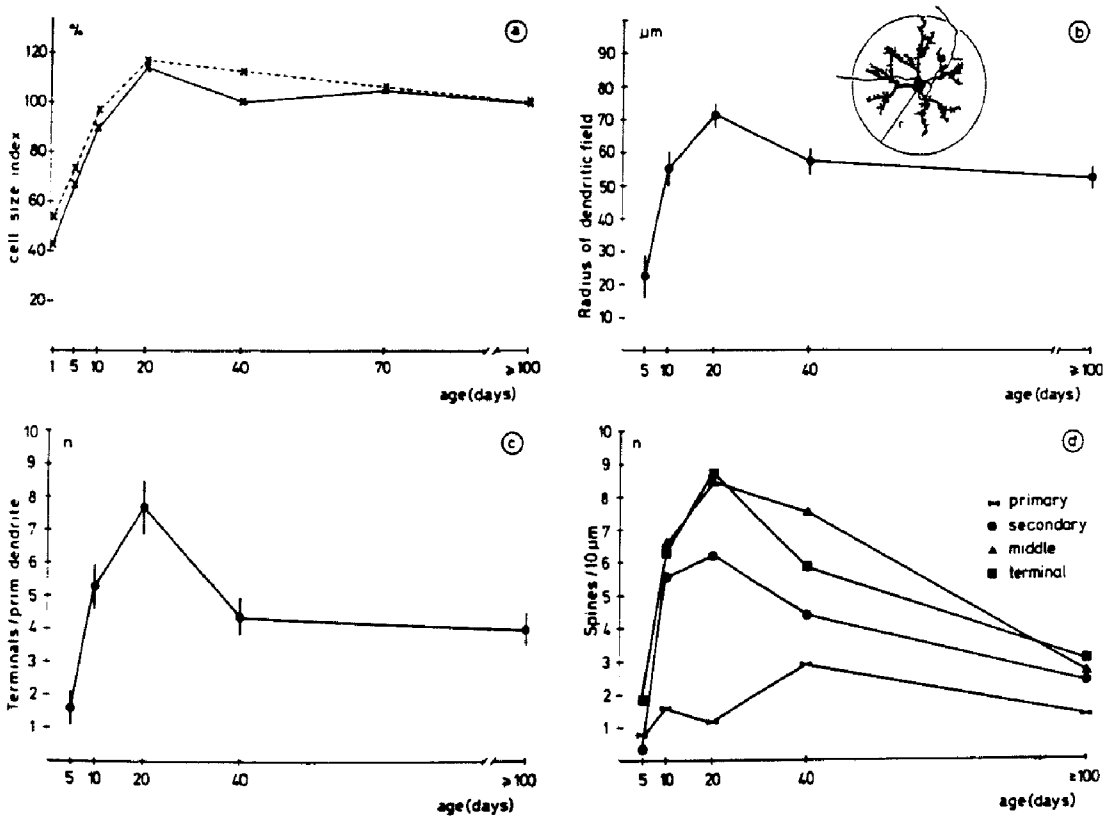

Fig. 3: Time course of development of different neuronal elements. a: neuron size (% of adult values). Stippled line: ectostriatum, full line: n. rotundus. After Herrmann and Bischof (1986a). b–d: ectostriatal measurements. b: Number of terminal segments per primary dendrite, c: average radius of dendritic field, d: Number of spines per µm for different segments of the dendrite. Primary: segments directly adjacient to the cell body, secondary: segments following the primary ones, terminal: end segments of each dendrite; medial: segments which were not primary or terminal. After Herrmann and Bischof (1988b).

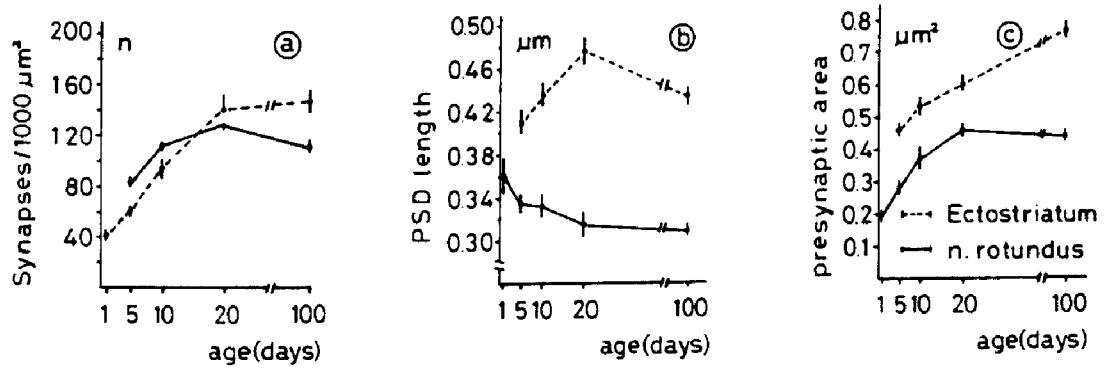

Fig. 4: Development of ultrastructural parameters of synapses in the n. rotundus (solid line) and ectostriatum (stippled line) a: average number of synapses/1000 μm^2 neuropil, b: length of postsynaptic densities (μm), c: average size of presynaptic areas (μm^2). After Nixdorf (1988).

period. The features of the neurons on the «deprived» side, that is the hemisphere contralateral to the deprived eye, were compared with those of the «nondeprived» side and with values obtained from normally reared birds. Fig. 5 depicts the effects of monocular deprivation on soma size of n. rotundus neurons (Herrmann and Bischof, 1986c). After 20 days of monocular deprivation there is an increase on both the intact and the deprived hemisphere compared with values for normally reared birds.

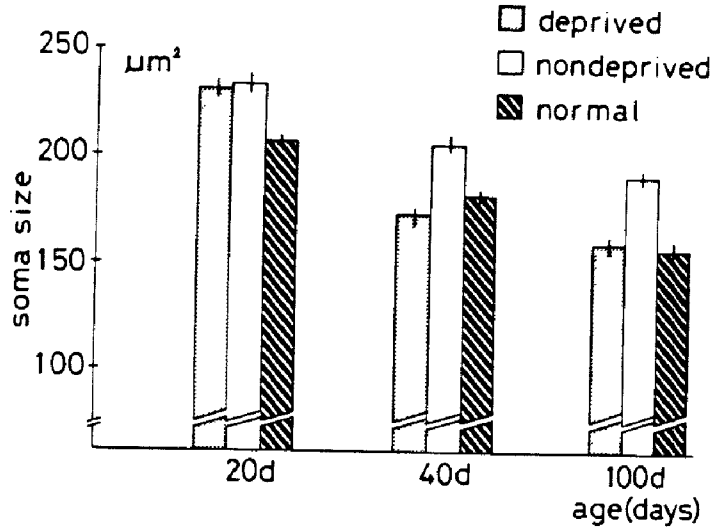

Fig. 5: Effects of different times of monocular deprivation (20, 40, 100d) from birth on neuron size of n. rotundus. After Herrmann and Bischof (1988b)

Deprivation for 40 or 100 days causes a significant hemisphere difference in soma size: neurons on the deprived side are 15% smaller than those on the nondeprived side. This interhemispheric difference, however, is not due to a shrinkage of neurons on the deprived side, but rather a result of a hypertrophy of cells in the nondeprived n. rotundus. The same effects can be observed in the ectostriatum of birds deprived for 20, 40 or 100 days (Herrmann and Bischof, 1986b).

Analysis of Golgi preparations of the ectostriatum (Herrmann and Bischof, 1988b) reveals that deprivation from birth has no significant effect on either the development of the dendritic field or on the number of terminals per primary dendrite. In each measurement and for each age group, the values of the deprived and the non-deprived hemisphere of MD-animals do not differ significantly from those of normally reared birds of the same age.

In contrast, the number of spines per 100 μm dendritic length is severely affected if the duration of the deprivation is 40 or 100 days. The effects are different for the different sections of the dendrites (Fig. 6). In general, spine density is significantly lower in the deprived hemisphere than in the nondeprived hemisphere. However, taking the naturally occurring spine loss of neurons of normally reared birds into consideration, it seems that the hemispheric difference is due to a lack of spine reduction in the non deprived hemisphere as well as to an enhanced loss in the deprived hemisphere: After long term deprivation the number of spines does not differ from normally reared birds, whereas the spine number in the nondeprived hemisphere is larger.

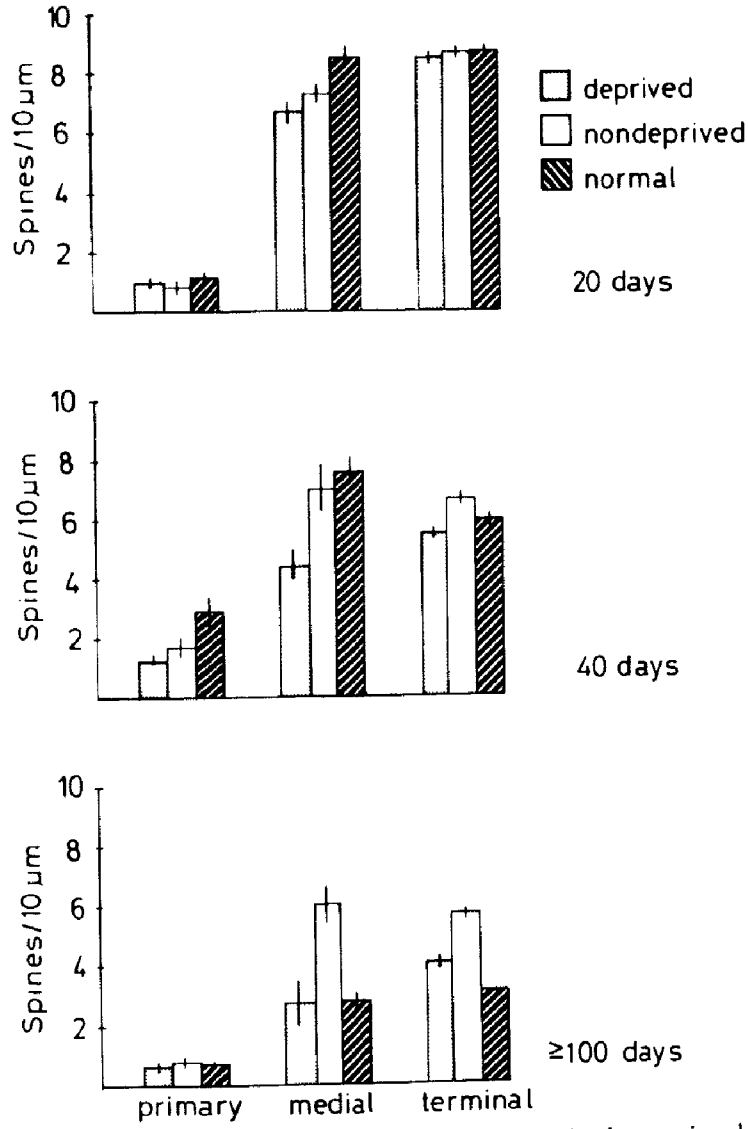

Fig. 6: Effects of monocular deprivation for different times from birth on spine density of primary, medial, and terminal segments of ectostriatal neuron dendrites. After Herrmann and Bischof (1988b)

Ultrastuctural effects of monocular deprivation were observed in birds deprived from birth for 20 and 100 days, respectively (Nixford and Bischof, 1987, Nixdorf, 1987). The number of synapses/1000 μm^2 of n. rotundus was larger in both hemispheres of birds deprived for 20 days than in normally reared animals. This enhancement could be observed after 100 days only in the deprived hemisphere (Fig. 7a). The reverse effect is observed for the size of the presynaptic area. After 20 days of deprivation, the average size of presynaptic areas was smaller on both sides, in 100 day old birds only on the deprived side (Fig. 7b). No effect could be observed on the length of postsynaptic thickenings.

For the ectostriatum, no effect could be observed concerning the number of synapses. Presynaptic areas were smaller in both hemispheres with 20 and 100 days of deprivation (Fig. 7c). The same basic effect could be observed for the postsynaptic thickenings but the reduction was significantly stronger on the deprived side and the effect was not significant in 100 day old birds (Fig. 7d).

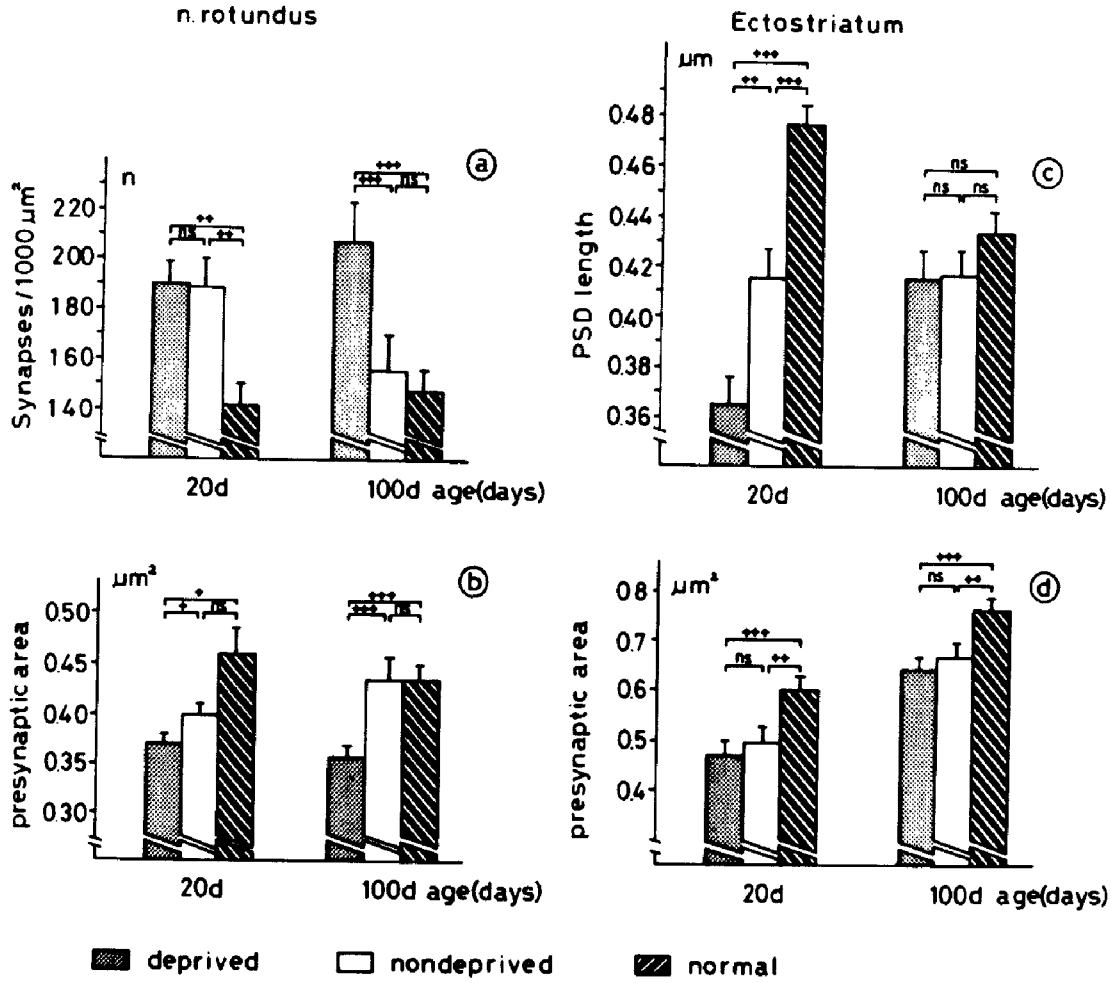

Fig. 7: Effects of monocular deprivation for 20 or 100 days from birth. left side: n. rotundus, right side: ectostriatum; a: average number of synapses/1000 μm^2 neuropil. b: size of presynaptic area; c: length of postsynaptic densities. d: size of presynaptic area. Note that only b. and d. are directly comparable. After Nixdorf and Bischof (1987) and Nixdorf (1987)

5. The sensitive period

For these measurements, cell size was measured in birds subjected to 40 days of unilateral eye closure starting at ages spaced regularly throughout the first 70 days of age (Herrmann and Bischof, 1988a). Fig. 8 shows the difference of cell size between the deprived and the undeprived hemisphere of the different age groups. It demonstrates that monocular deprivation markedly affects cell size in the n. rotundus and ectostriatum if the treatment starts at one or ten days posthatch. The differences between deprived and nondeprived neurons decline monotonically with increasing visual experience prior to deprivation. However, deprivation from 40 days of age causes as severe an effect as monocular closure at birth, whereas deprivation from day 50 or later no longer leads to abnormalities. These data indicate that the sensitive period for the effects of monocular deprivation may be double-peaked:the sensitivity for external stimuli declines from hatch until day 30, but has another peak at about 40 days of age. Thereafter, no influence of environmental changes on neuronal development can be observed.

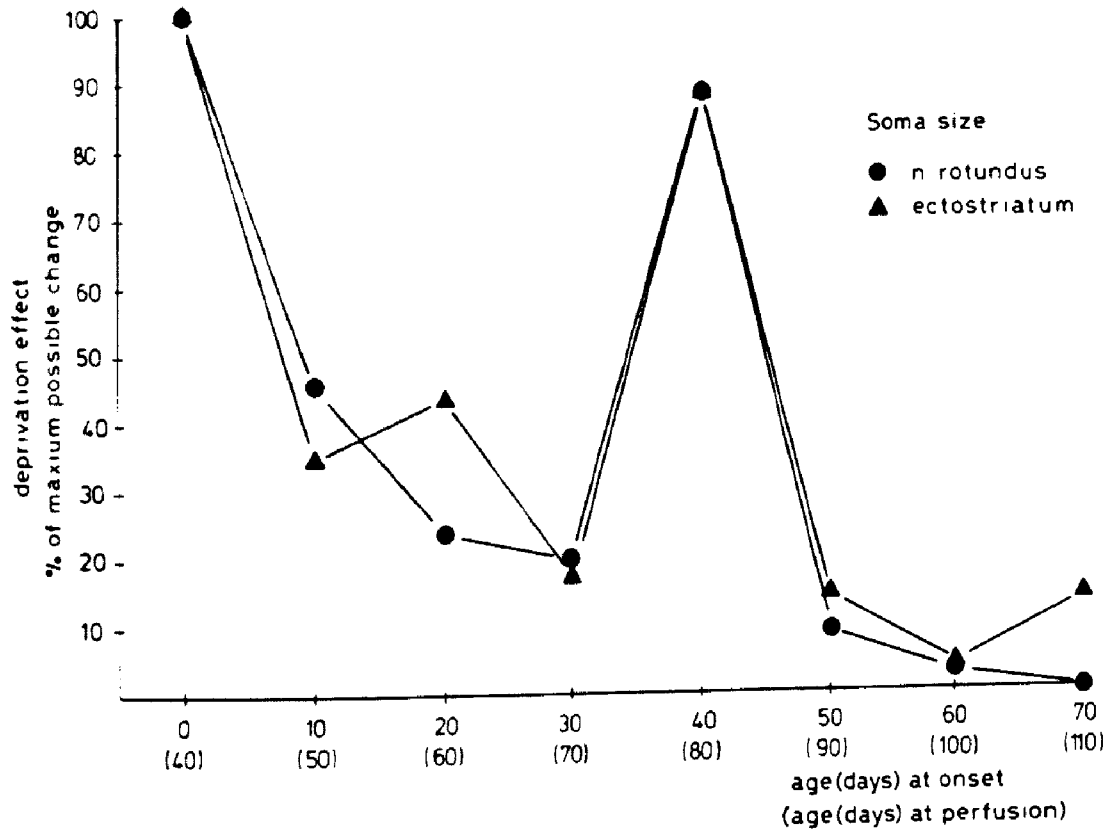

Fig. 8: Sensitive period for the effects of monocular deprivation derived from left-right differences in the deprived birds. The difference between neonatally deprived birds was set at 100%. After Herrmann and Bischof (1988a).

Discussion

The results presented above demonstrate that the development of the different neuronal elements and the effect of monocular deprivation on the morphology of the tectofugal pathway is not uniform. However, instead of going into the details, I want to concentrate here on some general features of our results and to discuss their significance to theories of the neuronal basis of imprinting as well as their relations to other studies.

General effects of monocular deprivation in birds

The effects of monocular deprivation are different between the two nuclei and the different times of treatment. The overall pattern of these changes is not simple enough to allow a consistent and full interpretation. However, our results clearly show that there are some general effects of monocular deprivation.

In most cases, two stages of deprivation effects can be observed. By shorter deprivation periods, both sides of the brain are affected by the treatment, reacting either with an increase or with a decrease of the measures of number or size of neuronal elements. Longer lasting deprivation between 40 and 100 days in most cases leads to an adjustment of the measures within one or the other hemisphere of the deprived birds, when compared with values of normally raised animals. These effects, namely the variation in the increase and

decrease of the measurements and the involvement of both hemispheres, were quite unexpected. If birds have largely independent tectofugal systems on both sides of the brain, as earlier studies stated, no effect should be observed at the contralateral hemisphere, and the main effect of deprivation should be a shrinkage of neurons and neuronal elements, as was observed for example in the monocular segment of the cat geniculate body (Cragg et al., 1975).

In contrast, our results indicate that the two hemispheres interact in the reaction to monocular deprivation. In some cases, the nondeprived hemisphere seems to enhance the size and amount of neuronal elements, perhaps in order to compensate for the lack of visual input to one eye by enlarging the stimulus processing capacities of the intact hemisphere. Most probably, the interaction between the two sides implies some sort of competition process between the two hemispheres, as was demonstrated for the development of neurons of the visual cortex of mammals (rev. Fregnac and Imbert, 1984). However, this competition process should have a different goal than to align the visual fields of the both eyes during development, as was proposed for animals with frontally placed eyes: zebra finches are birds with laterally placed eyes and only very small binocular overlap (Bischof 1988). Interestingly, no substantial deprivation effects (except small shrinkage of LGN neurons as direct consequence of deprivation) could be demonstrated in mammals with laterally placed eyes like rabbits (Chow and Spear, 1974), or in the monocular segment of cats (Hickey et al., 1977). Again this demonstrates that in birds competition processes of as yet unknown function may play a role in development of the visual centers.

Recent anatomical and electrophysiological experiments from our lab have demonstrated that the hemispheric interactions which may induce these competion processes are due to a massive projection leading from the tectum opticum to the contralateral n. rotundus (Brinkkötter and Bischof, 1987; Niemann et al, 1987). Electrophysiological experiments show in addition that the reaction of the ectostriatum to ipsilateral eye stimulation is substantially suppressed by the contralateral eye (Engelage and Bischof, 1988).

Neuronal development and imprinting

Most of our measurements demonstrate that neuronal elements grow rapidly until day 20. Thereafter, the size and number of neuronal elements decrease until day 40, when they reach their adult size in most cases. This peak-decline trend (Murphy, 1984) can be observed in a variety of animals and for many different neuronal elements (for review see: Herrmann and Bischof, 1988b), and therefore seems to be a common feature of neuronal development. Most theories of brain development argue that this overproduction of neuronal connections is due to the fact that it is not possible for the genetic program to exactly define the needs of the nervous system for optimal processing of stimuli from the environment. Therefore, a redundant system is built which is shaped to its final form under the influence of environmental stimulation. The reduction of the redundant network is accomplished by a selection process which favours functionally efficient neuronal connections over those which cannot be driven efficiently by the periphery (Hebb, 1949, Hubel and Wiesel, 1965, Changeux and Danchin, 1976).

Most of these theories are based on work on the visual cortex in cats and monkeys. However, researchers in the field of imprinting and song learning have adopted this view. On the behavioral level, Marler and Peters (1982) demonstrated that song sparrow have a larger repertoire during the time of song crystallization than they have later as adults. Rausch and Scheich (1982) examined the development of spines in a song control nucleus in mynah birds, and found a reductioin of spine elements at the time when the bird learns

its songs and imitations for example of human voice. Wallhäußer and Scheich (1987) found a reduction of spines in an area of the forebrain of chicks as a consequence of an imprinting procedure. They interpreted their findings to show that the acoustic input during the imprinting procedure leads to a shaping process which favours the processing of imprinted information by selective stabilisation of those synapses which are used in this context, and a reduction of the uneffective synaptic connections. The stabilization of the connections which are selected may be indicated by the results of Horn and coworkers (rev. Horn, 1985), who demonstrated that in another area of the chick forebrain, which is probably involved in imprinting, the postsynaptic thickenings of synapses of the left hemisphere increased in length after imprinting.

Possibly, the physiological events underlying sexual imprinting in zebra finches may be similar to those observed in the above mentioned paradigms, namely the shaping of neuronal responses in the visual cortex of cats, song learning, or filial imprinting, respectively (Bischof 1983, 1985a). If this is true, sexual imprinting should occur during the time where a reduction of neuronal connections can be observed. However, our results demonstrate that the peak of neuronal development and the decline of size and connections of neuronal elements is delayed for some time, compared to the sensitive period for sexual imprinting (Fig. 1). This means that the behavioral effects of sexual imprinting (the preference for a given subject) can be observed at the time where the brain elements develop rapidly, and not at the time of elimination of neuronal connections, as it was presumed in the above mentioned paradigms.

However, this does not necessarily mean that sexual imprinting has an other physiological basis than the paradigms mentioned above. One has to keep in mind that the parameters we measured in our studies were morphological ones, whereas the sensitive period for sexual imprinting was determined by measurements of behavioral change. It is conceivable that this behavioral change is accompanied by physiological changes of the neuronal network, for example by alterations of the transmission of synapses. These physiological changes may lead to an altered inhibition-excitation balance of neuronal input (Wolff, 1981); and this alteration in the balance of neuronal input may induce, with a certain delay, the reduction of redundant neuronal elements, as it can be seen in our developmental studies.

Our deprivation experiments show that the sensitive period for monocular deprivation is very similar to that obtained for sexual imprinting (Fig. 1). This again underlines that the physiological events observed in the development of cortical neurons may well be similar to those underlying sexual imprinting.

Imprinting as part of a common developmental process

The idea that imprinting may be only a small part of the global process, by which the nervous system is tuned during development under the guidance of information from the external environment (Bischof 1983, 1985a, b), may explain why effects of imprinting have been observed in very different regions of the bird's brain. Horn and Coworkers (rev. Horn, 1985) favoured an area of the forebrain called IMHV (part of hyperstriatum ventrale) as a candidate for the storage of imprinted information in filial imprinting. However, they demonstrated that other parts of the brain are also involved in the storage process. Salzen et al (1975) showed that the lateral neostriatum is involved in filial imprinting, and Scheich and coworkers (rev. Scheich, 1988) demonstrated that part of the intermedial neostriatum/hyperstriatum (MNH) is affected by filial imprinting. In mammals it has even been demonstrated that effects of odor imprinting can be observed in the olfactory bulb (rev. Apfelbach, 1986).

As sexual imprinting in birds is a process which is predominatly visually guided (Bischof, 1985c), we suspected that during imprinting neurons of visual centres of the brain are tuned to optimally process the stimuli which are learned by imprinting, such as the features of conspecific females. Our results demonstrate that n. rotundus and ectostriatum can be affected by changes of environmental stimulation at the time where imprinting occurs, and therefore it may well be that imprinting really is based on the process of tuning of neuronal elements of the ectostriatum and n. rotundus.

However, I do not want to suggest that the ectostriatum and the n. rotundus are the main places where imprinted information is stored. Herrmann (unpublished) has shown that some other forebrain areas develop in parallell to the ectostriatum. Moreover, we have demonstrated (Bischof and Herrmann, 1986) that four forebrain areas other than the ectostriatum are activated, besides other arousing stimuli, by the appearance of a female, the stimulus configuration which had been imprinted during the sensitive period. Therefore, it is much more likely that imprinting does not alter the connectivity of only one or two areas of the birds brain, but alters connections in a variety of brain regions, as mentioned above.

Final remarks

At least, one statement has to be made about plasticity of the brain in general. For a long time, the commonly held view was that the brain of young animals is very flexible in the sense that connections between neurons can easily be made or be destroyed. In contrast, the adult brain was seen as quite stable and quite unchangable. Therefore developmental plasticity and imprinting have often be seen as consequences of the plasticity of young brains. Purves et al. (1986), however, demonstrated that even in the adult brain the neurons change connections permanently. So, the question is not how the nervous system gains plasticity during sensitive periods, but how it achieves stability outside of the sensitive periods. For our results this does mean that increases or decreases or periods of no change may be induced by a balance between construction and destruction of neuronal connections. If we see an increase in our snapshot like preparations, the construction overcomes the destruction and the reverse occurs if we see a decrease of neuronal elements.

The question remains as to how the nervous system «knows» the stage of development at which it has to consider external influences in this turnover process, and at what time it has to try to leave the logics of connectivity unchanged. Perhaps, these considerations may help to find explanations for the findings which are not discussed earlier in the paper: Why, for example, is the visual system a second time alterable by external input at about 40 days of age as we have shown, and why, in contrast to mammals, is the adult brain of birds modifiable at least periodically, as it was shown for the song system (Nottebohm, 1985).

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Summary

For mammals it is well established that alteration of the visual input during early development leads to changes in the wiring of neurons in the visual cortex. By contrast, little is known about how changes in the external environment affect the development of visual centers of the bird's brain. My research group and I were interested to investigate this phenomenon, because the developmental plasticity of cortical neurons in mammals has many features in common with imprinting (rev. Bischof, 1983, 1985). Imprinting is a special learning process by which young birds develop social and sexual preferences for the first individuals they encounter. Both imprinting and cortical plasticity occur during a restricted period early in life, the sensitive period, and the information stored is remarkably stable. Given these and other parallels it seems likely that neuronal events similar to those which are described in visual cortex development of mammals may well occur in the bird's brain during imprinting.

We therefore followed the normal development of neurons in two areas of the tectofugal pathway of the zebra finch, a small altricial bird which is commonly used in imprinting studies. In addition, we investigated the effects of monocular deprivation on the development of the neurons of these areas. Our results show that in normal development an overshoot of nearly all investigated features of neurons occurs at 20 days of age, followed by a decrease until 40 days of age. Monocular deprivation affects the development of both hemispheres, indicating strong interactions between the two sides of the brain. The sensitive period for the effects of monocular deprivation is double-peaked. The first peak roughly coincides with the sensitive period for sexual imprinting. However, for the second peak we have not found a behavioural correlate as yet.

The compatibility of our results to those found in mammals, to recent theories of neuronal plasticity, and to the results of other groups investigating the neural basis of imprinting, will be discussed.

References

Apfelbach, R. (1986): Imprinting on prey odours in ferrets (Mustela putorius L.) and its neuronal correlates. Behav. Processes *121*, 363–382.

Bagnoli, P., Porciatti, V., Fontanesi, G., Sebastiani, L. (1987): Morphological and functional changes in the retinotectal system of the pigeon during the early posthatching period. J. comp. Neurol. *256*, 400–411.

Bischof, H.-J. (1983): Imprinting and cortical plasticity: A comparative review. Neurosci. Biobeh. Rev. *7*, 213–225.

Bischof, H.-J. (1985): Der Anteil akustischer Komponenten an der Auslösung der Balz männlicher Zebrafinken (Taeniopygia guttata castanotis). J. Orn. *126*, 273–279.

Bischof, H.-J. (1985a): Environmental Influences on Early Development: A comparison of imprinting and cortical plasticity. In: Perspectives of Ethology, Vol. 6: Mechanisms (P. Bateson, P. Klopfer, eds.), pp. 169–217. Plenum, New York.

Bischof, H.-J. (1985b): Influence of Developmental Factors on Imprinting. In: Brain Plasticity, Learning, and Memory (B. E. Will, P. Schmitt, J. Dalrymple-Alford, eds.), pp. 51–59, Plenum, New York.

Bischof, H.-J. (1988): The visual field and visually guided behavior in the zebra finch. J. comp. Physiol. A *163*, 329–337.

Bischof, H.-J., Lassek, R. (1985): The gaping reaction and the development of fear in young zebra finches. Z. Tierpsychol. *69*, 55–65.

Blakemore, C., VanSluyters, RC. (1974): Reversal of the physiological effects of monocular deprivation in kittens: Further evidence for sensitive period. J. Physiol. (Lond.) *237*, 195–216.

Brinkkötter, I., Bischof, H.-J. (1988): Light- and Electron Microscopic Analysis of the Tecto-Rotundal Visual Projection in the Zebra Finch. In: Sense Organs, Interfaces between Environment and Behavior (N. Elsner, F. G. Barth, eds). Thieme, Stuttgart, New York, 257.

Changeux, JP., Danchin, A. (1976): Selective stabilization of developing synapses as a mechanism for the specification of neuronal networks. Nature *264*, 705–712.

Chow, KL., Spear, PD. (1974): Morphological and functional effects of visual deprivation on the rabbit visual system. Expl. Neurol. *42*, 429–447.

Cragg, B. (1975): The development of synapses in kitten visual cortex during visual deprivation. Exp. Neurol. *46*, 445–451.

Cragg, B., Anker, R., Wan, YK. (1975): The effect of age and reversability of cellular atrophy in the LGN of the cat following monocular deprivation: A test of two hypotheses about cell growth. J. comp. Neurol. *168*, 345–354.

Engelage, J., Bischof, H.-J. (1988): Enucleation enhances ipsilated flash evoked responses in the ectostriatum of the zebra finch (Taeniopygia guttata castanotis Gould). Exp. Brain Res. *70*, 79–89.

Fregnac, Y., Imbert, M. (1984): Development of neuronal selectivity in primary visual cortex of cat. Physiol. Rev. *64*, 325–434.

Hebb, D. O. (1849): The organization of behavior. Wiley, New York.

Herrmann, K., Bischof, H.-J. (1986): Delayed development of song control nuclei in the zebra finch is related to behavioral development. J. comp. Neurol. *245*, 167–175.

Herrmann, K., Bischof, H.-J. (1986): Monocular deprivation affects neuron size in the ectostriatum of the zebra finch brain. Brain Res. *379*, 143–146.

Herrmann, K., Bischof, H.-J. (1986): Effects of monocular deprivation in the nucleus rotundus of zebra finches: A deoxyglucose and Nissl study. Exp. Brain Res. *64*, 119–128.

Herrmann, K., Bischof, H.-J. (1988): The sensitive period for the morphological effects of monocular deprivation in two nuclei of the tectofugal pathway of zebra finches. Brain Res. *451*, 43–53.

Herrmann, K., Bischof, H.-J. (1988): The development of neurons in the ectostriatum of normal and monocularly deprived zebra finches: A quantitative Golgi study. J. comp. Neurol. *277*, 141–154.

Hickey, TL., Spear, PD., Kratz, KE. (1977): Quantitative studies of cell size in the cat's dorsal geniculate nucleus following visual deprivation. J. comp. Neurol. *172*, 265–282.

Horn, G. (1985): Memory, Imprinting, and the Brain. Clarendon Press, Oxford.

Hubel, DH., Wiesel, TN. (1965): Binocular interaction in striate cortex of kittens reared with artificial squint. J. Neurophysiol. *28*, 1041–1059.

Hubel, DH., Wiesel, TN. (1970): The period of susceptibility to the physiological effects of unilateral eye closure in kittens. J. Physiol. (Lond.) *208*, 419–436.

Immelmann, K. (1972): The influence of early experience upon the development of social behavior in estrildine finches. Proc. XVth Int. Orn. Congr., 317–338.

Karten, HJ. (1969): The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. Ann. N. Y. Acad. Sci. *167*, 164–179.

Kasamatsu, T., Heggelund, P. (1982): Single cell responses in cat visual cortex to visual stimulation during iontophoresis of noradrenaline. Exp. Brain Res. *45*, 317–327.

Marler, P., Peters, S. (1982): Developmental overproduction and selective attrition: New processes in the epigenesis of bird song. Devel. Psychobiol. *15*, 369–378.

Murphy, E. H. (1984): Critical periods and the development of the rabbit visual cortex. In: Development of visual pathways in Mammals (J. Stone, B. Dreher, D. H. Rappaport, eds.), pp. 429–462. Allan R. Liss, New York.

Niemann, J., Engelage, J., Bischof, H.-J. (1987): Rückkreuzende visualle Projektionen im tectofugalen System des Zebrafinken (Taeniopygia guttata castanotis). In: New Frontiers in Brain Research (N. Elsner, O. Creutzfeld, eds.) Thieme, Stuttgart, 166.

Nixdorf, BE., Bischof, H.-J. (1986): Posthatching development of synapses in the neuropil of nucleus rotundus of the zebra finch: A quantitative electron microscopic study. J. comp. Neurol. *250*, 133–139.

Nixdorf, B. (1986): Synaptogenese and Plastizität im tectofugalen System des Zebrafinken: Eine quantitative elektronen-mikroskopische Analyse. Thesis, Bielefeld.

Nixdorf, BE., Bischof, H.-J. (1987): Ultrastuctural effects of monocular deprivation in the neuropil of nucleus rotundus in the zebra finch: A quantitative electron microscopic study. Brain Res. *405*, 326–336.

Nottebohm, F. (1985): Neuronal replacement in adulthood. Ann. N. Y. Acad. Sci. *457*, 143–161.

Pettigrew, JD., Konishi, M. (1976): Effects of monocular deprivation on binocular neurons in the owl's visual wulst. Nature *264*, 753–754.

Purves, D., Hadley, RD., Voyvodic, J. (1986): Dynamic changes in the dendritic geometry of individual neurons visualized over periods up to three month in the superior cervical ganglion of the living mouse. J. Neurosci. *6*, 1051–1060.

Rausch, G., Scheich, H. (1982): Dendritic spine loss and enlargement during maturation of the speech control system in the mynah bird (Gracula religiosa). Neurosci. Lett. *46*, 131–136.

Salzen, EA., Parker, DM., Williamson, AJ. (1975): A forebrain lesion preventing imprinting in domestic chick. Exp. Brain Res. *24*, 145–157.

Scheich, H. (1987): Neural correlates of auditory filial imprinting. J. comp. Physiol. A *161*, 605–619.

Wallhäusser, E., Scheich, H. (1987): Auditory imprinting leads to differential 2-deoxyglucose uptake and dendritic spine loss in the chick rostral forebrain. Dev. Brain Res. *31*, 29–44.

Wiesel, T. N., Hubel, D. H. (1963): Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body. J. Neurophysiol. *26*, 978–993.

Winfield, D. A. (1983): The postnatal development of synapses in different laminae of the visual cortex in the normal kitten and kittens with eyelid suture. Dev. Brain Res. *9*, 155–169.

Wolff, J. R. (1981): Some morphogenetic aspects of the development of the central nervous system. In: Behavioral development: The Bielefeld Interdisziplinary Project. (K. Immelmann, G. W. Barlow, L. Petrinovich, M. Main, eds.); pp. 164–190. Cambridge Univ. Press, Cambridge.